

## *Psaenythisca*, a New Genus of Bees from South America (Apoidea: Andrenidae: Protandrenini) with a Description of the Nesting Biology and Immature Stages of One Species

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### ABSTRACT

A new bee genus from Argentina, *Psaenythisca*, is described and includes three species: *P. flavifrons* (Vachal, 1909), n. comb. (originally described as *Psaenythia*), *P. wagneri* (Vachal, 1909), n. comb. (originally described as *Psaenythia*), and *P. punctata* (Urban, 2009), n. comb. (originally described as *Anthrenoides*). The new genus is proposed based on a comparative study of the Protandrenini lineages. *Psaenythisca* is closely related to *Cephalurgus* and *Rhopitulus*, and can be distinguished mainly by the forewing with three submarginal cells, premarginal area of S2 to S5 of male with dense pubescence, distal margin of S6 of male slightly emarginated, and male genitalia with relatively broad basal sclerite. Among Protandrenini genera with three submarginal cells, it differs from *Anthrenoides* and *Psaenythia* by the combination of male genitalia with a basal sclerite, metasomal terga lacking yellow markings, propodeum rounded, middle tibial spur of the female finely serrate, and slender basal area of S8 of male. In addition, a lectotype is designated for *Psaenythia* (*Psaenythia*) *wagneri* Vachal, 1909. The holotype of *P. flavifrons* and the lectotype of *P. wagneri* are redescribed, and the female of *P. flavifrons* and male of *P. punctata* are described for the first time. An identification key to, and distribution maps of, the species of *Psaenythisca* are also provided.

Nearly a quarter of a century ago, Arturo Roig-Alsina and the second author discovered a communal nest of one of the species, now known as *Psaenythisca wagneri* (Vachal, 1909). The nest descended approximately 2 m into the ground and is described herein. From this nest,

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provision masses, eggs, larvae, and pupae were retrieved as well as developmental and behavioral information. The immatures are described and compared with those of related taxa, and the developmental and behavioral information are recorded. Of special interest is the fact that males exhibit a wide range of head sizes and head shapes. All of this gives rise to intriguing new questions for future investigation.

## INTRODUCTION

Protandrenini are a group of bees with more than 400 species described, restricted to the New World (Michener, 2007; Moure et al., 2007, 2012; Ascher and Pickering, 2014). The tribe is especially diverse in the temperate and xeric areas of the Americas, with a lower diversity in the mesic tropical forest (Michener, 2007). Most adults of the group have a relatively cylindrical and slender body and are specialized in collecting pollen from a restricted group of such plants as Asteraceae, Cactaceae, Malvaceae, Passifloraceae, Oxalidaceae, and Onagraceae (Neff and Rozen, 1995; Rozen, 1967, 1989; Schlindwein and Moure, 1998, 1999; Gaglianone, 2000; Gimenes, 2002). The nesting biology, immature stages, and cleptoparasites are known only for a few species of the tribe; all species are solitary or communal, with nests as burrows in the ground (Rozen, 1989; Ruz and Rozen, 1993; Neff and Rozen, 1995; Gaglianone, 2000; Chiappa et al., 2005).

Taxonomically, Protandrenini is a complex tribe with many new genera and species to be described especially in South America, and with several species incertae sedis that cannot be assigned to existing genera (e.g., Ruz and Chiappa, 2004; Ramos and Melo, 2006). Some Protandrenini genera are very species rich and lack recent taxonomic revisions, as the South American genera *Rhopitulus*, *Anthrenoides*, and *Psaenythia* (Ramos and Melo, 2010). Phylogenetic studies within Protandrenini are scarce and the current generic classification is precarious with controversial definitions of their genera (see Ruz, 1986; Ascher, 2004; Michener, 2007; Ramos, 2011; and Moure et al., 2012). As a contribution to our understanding of the tribe, a new genus of Protandrenini from Argentina is described, and information is included about the nesting and immature stages of one of its species. The new genus was originally recognized by J.S. Moure, who wrote the name *Psaenythisca* on labels attached to some old specimens of *Psaenythia wagneri* Vachal, 1909. However, its formal description was not provided by Moure. Over the years, this species and two others also described by Vachal (1909)—*Psaenythia flavifrons* and *Psaenythia nigrinasis*—have been traditionally included in *Psaenythia* or *Anthrenoides* (Holmberg, 1921; Neff and Rozen, 1995; Ascher, 2004), or considered as incertae sedis by Moure et al. (2007, 2012). Recently, the systematic study of the Protandrenini genera corroborated *Psaenythia flavifrons* and *Psaenythia wagneri* to be distinct from other genera of the tribe (Ramos, 2011; Ramos and Melo, in prep.), and *Anthrenoides punctatus* Urban, 2009, was congeneric with them. The description of the genus and designation of its type species, below, validates the generic name of *Psaenythisca* for these three species.

*Psaenythisca* is recognized by a unique combination of morphological characters, particularly in the hidden sterna and genitalia of males. A singular feature of the genus is the large basal sclerite on male genitalia. This particular structure is also found, though smaller in size, in *Cephalurgus*, *Chaeturginus*, and *Rhopitulus*, genera with two submarginal cells. It has been considered



homologous to the gonobase by many authors (see Michener, 2007), although it may have no direct relationship to the bee gonobase, which is absent in other Protandrenini, as pointed out by Ruz and Melo (1999). Another notable characteristic of *Psaenythisca* is cephalic polymorphism among males (males with small to large head sizes and various proportions), also known in some other Protandrenini from South America genera such as *Cephalurgus*, *Parasarus*, *Anthrenoides*, and *Psaenythia*. In Perditini, in which the polymorphism among males is more accentuated, macrocephalic, flightless males appear to have an advantage in grasping females for mating in the nest by having relatively larger heads and longer mandibles (Rozen, 1967; Danforth, 1989, 1991; Neff and Danforth, 1992; Norden et al., 1992; Michener, 2007).

In this paper, the first author (K.S.R.) provided the description of the genus based on adults, and the second author (J.G.R.) contributed the sections on nesting biology and immatures of *Psaenythisca wagneri* (Vachal).

## METHODS AND TERMINOLOGY

The adults studied are deposited in the following collections, with their respective curators in parentheses: AMNH, American Museum of Natural History, New York (Jerome G. Rozen, Jr.); DZUP, Coleção Entomológica Pe. J.S. Moure, Universidade Federal do Paraná, Curitiba, Brazil (Gabriel A.R. Melo); MZSP, Museu de Zoologia, Universidade de São Paulo, São Paulo, Brazil (Carlos R.F. Brandão); MNHP, Muséum National d'Histoire Naturelle, Paris, France (Claire Villemant).

The morphological terminology follows Urban (1967) and Michener (2007); the adult labral plate is understood as the central part of the labrum, characterized by an elevated and glabrous area. The term “macrocephalic” is used for males with increased head size and mandibular length, often diagnosable by direct comparison with several specimens. The antennal flagellomeres are indicated as F1, F2, etc.; the metasomal terga and sterna are, respectively, cited as T1–T7 and S1–S8. The density of punctation was based on the relative puncture diameter, *pd* (e.g., <2 *pd*: less than 2× the puncture diameter between punctures). All measurements are made based on the maximum width/length of the structure. Images of adults were obtained using a Leica videocamera DFC 295, attached to a Leica stereomicroscope M205C, and Leica LAS (Leica Application Suite V3.6.0) software to produce confocal images.

The labels of examined adult specimens are exactly transcribed in the sections Material Examined and Type Material, where one backslash (\) indicates a line break in the label, and double quotes indicate different labels associated with the same specimen. The lectotype designated here have been labeled as such. Distribution maps were produced using the software Quantum GIS (<http://www.qgis.org>) and the floral records for *Psaenythisca* species were compiled from the labels of the material examined.

Larvae, pupae, and eggs were preserved and stored in Kahle's solution until studied. For examination larval heads and bodies were separated and cleared of tissue by boiling in an aqueous solution of sodium hydroxide. After being washed in water, they were transferred to 70%–75% ethanol, stained with Chlorazol Black E, washed in ethanol, and submerged in glycerin on well slides for microscopic scrutiny and eventual storage. Pupae required no special

preparation. Eggs and larvae to be examined with a Hitachi S-4700 scanning electron microscope (SEM) were critical-point dried and then coated with gold/palladium.

Microphotographs of immature specimens and nest components were taken with a Canon PowerShot A2300, 16.0 megapixels, hand held, through one lens of either a Leitz Wetzlar stereomicroscope or a Carl Zeiss compound microscope.

## SYSTEMATICS

### TRIBE PROTANDRENINI ROBERTSON, 1904

#### *Psaenythisca* Ramos, new genus

TYPE SPECIES: *Psaenythia* (*Psaenythia*) *wagneri* Vachal, 1909.

DIAGNOSIS AND COMMENTS: *Psaenythisca* is recognized by a unique combination of morphological characters: forewing with three submarginal cells; males with compound eyes that diverge below; females with convex vertex (in frontal view); apical margin of male clypeus with developed projection just outside lateral labral margin; propodeum rounded, without flat and deep dorsal area; scopa with sparse simple hairs; hind femur of males with posterior margin toothed; T7 of males without pygidial plate; metapostnotum shallow with few longitudinal striae; male S6 slightly emarginated on middle portion of distal margin; premarginal area of S2 to S5 of male with dense plumose hairs; S6 of male slightly emarginated on distal margin; genitalia of male with broad basal sclerite; and S8 with slender basal portion and broad lateral apodeme. Females of *Psaenythisca* are quite similar and can be differentiated principally by body punctation and pilosity, while the males are recognized by the particular head morphology for each species.

The new genus shares features with South America genera *Cephalurgus*, *Chaetuginus*, and *Rhopitulus*, especially the basal sclerite on the male genitalia, and a deep oblique impression on the side of the male gonocoxite. Among these genera, *Psaenythisca* can be distinguished mainly by the forewing with three submarginal cells, the premarginal area of S2 to S5 of the male with a dense plumose pubescence, and the distal margin of S6 of the male slightly emarginated. Among the Protandrenini with three submarginal cells, *Psaenythisca* resembles *Anthrenoides* and *Psaenythia* in having large yellow marks on the male head. However, the male S8 has a slender basal portion and broad lateral apodeme, and male genitalia has a basal sclerite. Additionally, the new genus differs from *Psaenythia* by the metasomal terga lacking yellow markings, the middle tibial spur of the female finely serrate, the inner surface of the female hind femur without a longitudinal ridge, and the metasomal terga with sparse punctures. *Psaenythisca* can be distinguished from *Anthrenoides* mainly by the deep lateral fovea of T2, rounded propodeum (without flat dorsal surface), and slightly emarginated S6 of the male. Although the present paper was not intended to determine the phylogenetic relationships of *Psaenythisca* to other Protandrenini, characters related to the conspicuous male terminalia may be informative in phylogenetic studies. A putative autapomorphic feature of the new genus is the larger basal sclerite on the male genitalia in relation to the small structure present on *Cephalurgus*, *Chaeturginus*, and *Rhopitulus*.

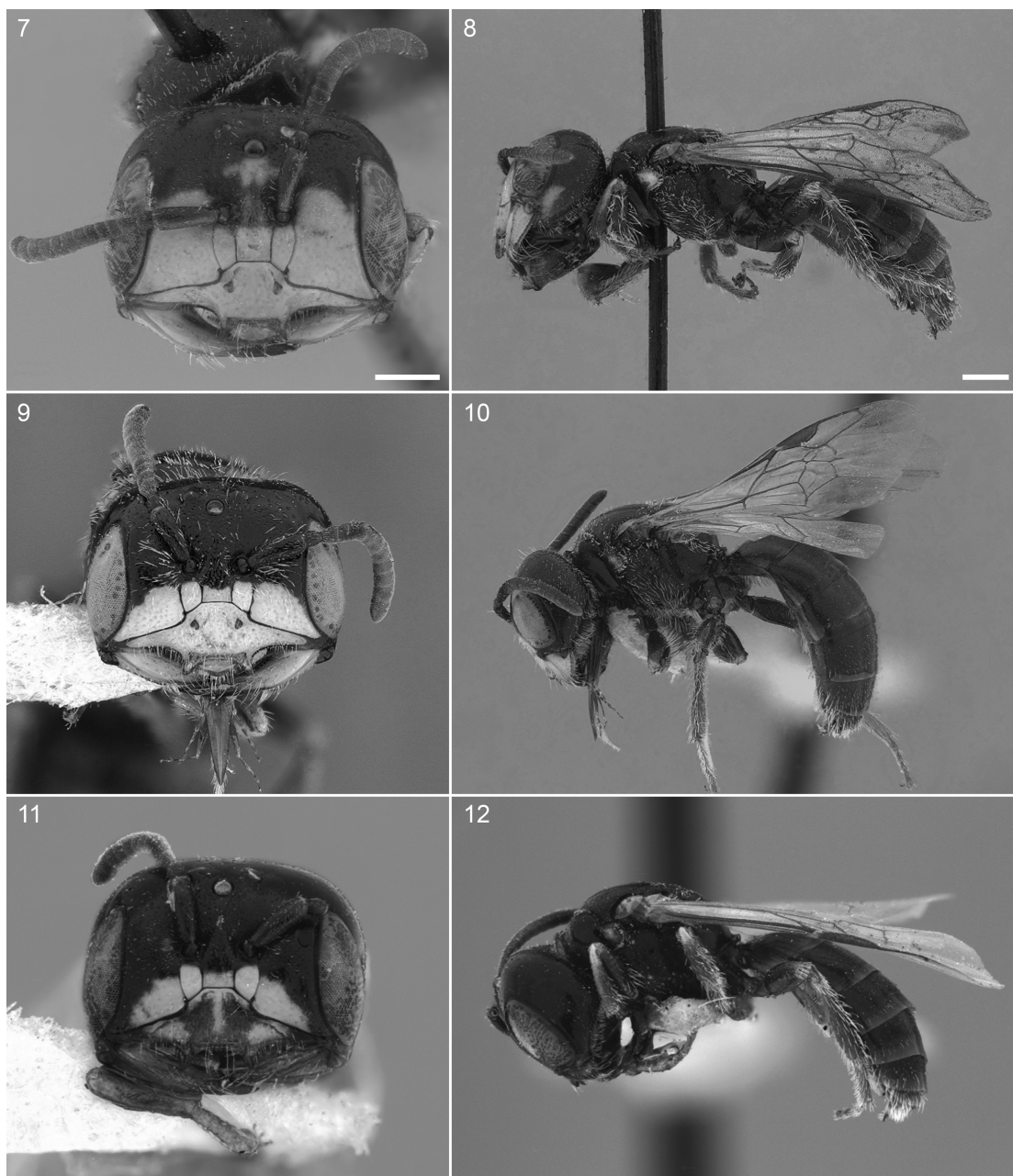
**DESCRIPTION:** Small bees, body length between 4.0 to 5.5 mm. Females with black to brownish body and yellow markings restricted to small spots between femur and tibia of fore- and midlegs. Spurs, wing veins, and tarsus light brown; tegula and marginal zone of metasoma translucent brown. Pubescence predominantly semidecumbent, short, sparse, and whitish in both sexes, with dense and plumose hairs on pronotal collar, scutellum, mesepisternum, lateral corners of propodeum, and metasomal sterna (males). Head with sparse short hairs and few longer setae between ocelli (as long as ocellar diameter); mandible and distal margin of clypeus with long and simple setae; labrum with short and simple setae, except for glabrous labral plate; eyes glabrous; ventral portion of gena of males with dense, short, and plumose pubescence. Metepisternum with minute hairs; metapostnotum with some few minute hairs on lateral portions; forewing with three submarginal cells; posterior portion of forefemur of males with long (about  $3.5\times$  ocellus diameter), erect, and finely branched pilosity; hind tibia of males with sparse and fine hairs; female with loose midfemoral brush; female hind tibial scopa loose with long and simple setae; basitibial plate of males with a few coarse and short setae on basal half. Disc of metasomal terga with very short, finely branched setae (fainter on T1 and T2); premarginal line of female terga with sparse, branched, decumbent, and long hairs (weakly developed in males); T5–T6 of female with prepygidial and pygidial fimbria sparse; T7 of males with sparse hairs and longitudinal glabrous line; premarginal area of S1–S5 with abundant decumbent plumose hairs directed toward the middle (stronger on S4 and S5); distal half of metasomal sterna of females with sparse, long, erect, simple setae; marginal zone of metasoma glabrous. Integument surface largely smooth and shiny between punctures, with predominantly fine and sparse punctures (varying from 1–3 pd), and coarse punctation on clypeus, around ocelli, and mesepisternum. Labral plate smooth and shiny. Pronotal collar, mesepisternum, metepisternum, and propodeum reticulated; metapostnotum with a few longitudinal striations. Metasomal terga slightly reticulated with fine punctures; marginal zone smooth on males and reticulated on females; pygidial plate of females strongly reticulated; sterna of male mostly shiny, with light reticulation and dense piligerous punctures on distal portion; sterna of females shiny and slightly reticulated between punctures. First labial palpomere as long as the length of three distal palpomeres combined; maxillary palpus with six subequal palpomeres; tentorial pit in intersection between outer subantennal suture and epistomal sulci; antenna slightly longer than head width, similar in both sexes; facial fovea and lateral fovea of T2 deep; vertex in frontal view slightly convex (straight on macrocephalic males); mesoscutum with mid and parapsidal lines evident; episternal groove extending below scrobal groove into omaulus area; forewing with three submarginal cells; pterostigma clearly wider than prestigma, margin within marginal cell convex; marginal cell truncate at apex and longer than the distance from its apex to wing tip; apex of tibia of males with small acute projection; tarsal claws distinctly bifid; hind tibia of male toothed on upper margin; female with pygidial plate V-shaped; S6 of male slightly emarginated on distal margin; S8 with slender basal portion and broad lateral apodeme; genitalia of male with broad basal sclerite; and male gonocoxite with deep oblique impression.

**VARIATION:** The males of *Psaenythisca* exhibit a cephalic polymorphism with small- to large-headed males occurring in all species. The macrocephalic specimens possess sparser punctures and pubescence, longer mandibles, vertex swollen above ocelli, and larger gena in



FIGURES 1–6. Females of *Psanythisca*, new genus. 1. *P. flavifrons* head in frontal view (from Otamendi). 2. *P. flavifrons* lateral habitus. 3. *P. punctata* head in frontal view (from Hurlingam). 4. *P. punctata* lateral habitus. 5. *P. wagneri* head in frontal view (from San Pedro de Colalao). 6. *P. wagneri* lateral habitus. Scale bars = 0.5 mm.





FIGURES 7–12. Macrocephalic males of *Psaenythisca*, new genus. 7. *P. flavifrons* (holotype) head in frontal view. 8. *P. flavifrons* (holotype) lateral habitus. 9. *P. punctata* head in frontal view (from Villaguay). 10. *P. punctata* lateral habitus (from Villaguay). 11. *P. wagneri* head in frontal view (from Otamendi). 12. *P. wagneri* lateral habitus (from Otamendi). Scale bars = 0.5 mm.

contrast to males with smaller heads (figs. 91,92). Additional information concerning male polymorphism is presented in the Discussion.

FLOWER RECORDS: The few flower records for *Psaenythisca* suggest that its species are associated with flowers of Malvaceae, with females and males of *P. wagneri* collected on *Sphaeralcea*.

DISTRIBUTION: The new genus is restricted in distribution to the Chacoan subregion of Neotropical region, along the northern portion of Argentina.

ETYMOLOGY: The name of the newly proposed taxon is a combination of the word *Psaenythia* (a bee genus that it closely resembles) plus the suffix *-isca*, which means "small, little." *Psaenythisca* is herein maintained in tribute to Jesus Santiago Moure, who originally recognized the need of its formal description and wrote this name on labels attached to specimens examined in this study. The gender is feminine.

#### KEY TO THE SPECIES OF *PSAENYTHISCA*, N. GEN.

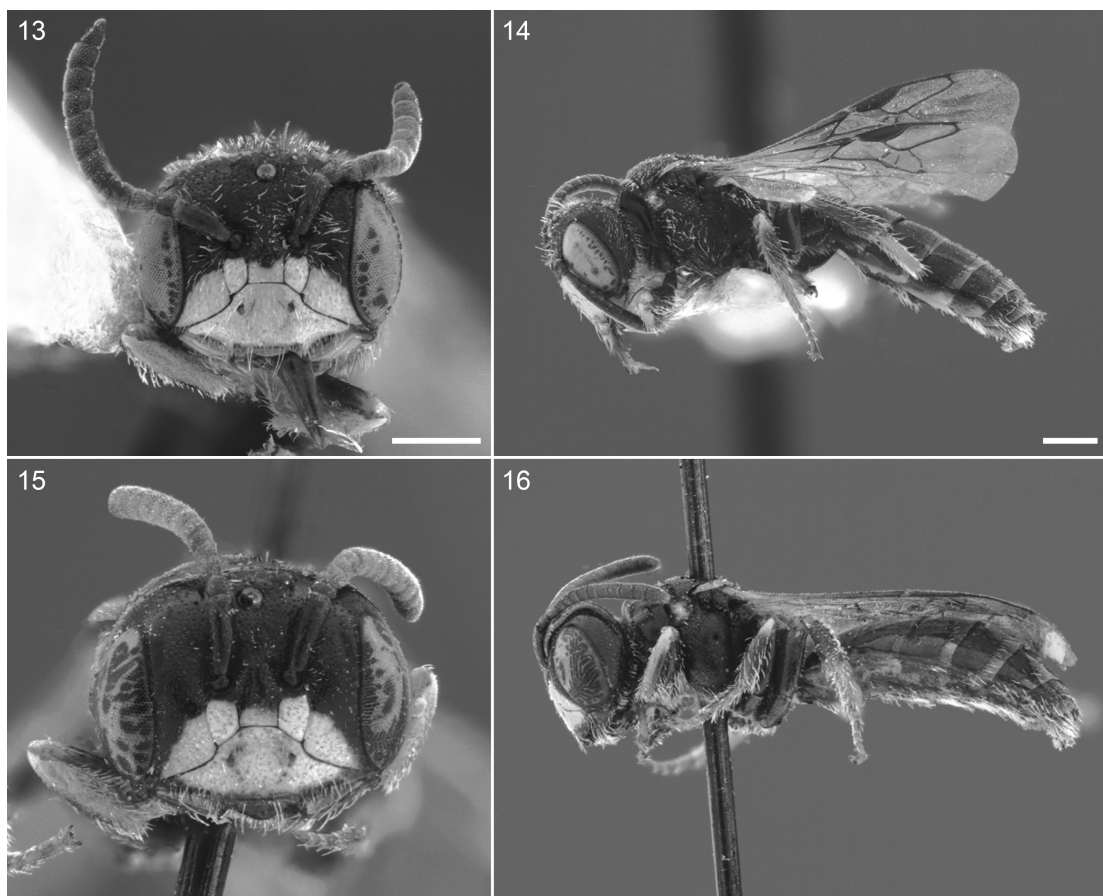
1. Female: clypeus, paraocular, and supraclypeal area reticulated between punctures (fig. 5); mesoscutum and scutellum with dense punctures (<1.5 pd) (fig. 19); basal portion of fore- and midtibia light brown. Male: second submarginal cells on forewing subtriangular, 1r-m and 2r-m strongly convergent (fig. 38); mandible and labral plate light brown (figs. 11, 15); clypeus mostly yellow with small areas light brown (fig. 11); lower paraocular area usually black near compound eyes (figs. 11, 15) .....*P. wagneri* (Vachal, 1909)
- Female: clypeus, paraocular, and supraclypeal area smooth and shiny between punctures; mesoscutum and scutellum with sparse punctures (>2 pd); basal portion of fore- and midtibia yellow. Male: second submarginal cell on forewing quadrangular, 1r-m and 2r-m subparallel (fig. 37); mandible (except for black apex), labral plate, clypeus, and lower paraocular area yellow .....2
2. Female: lateral fovea of T2 ellipsoid (fig. 23); head with coarse punctures, mainly on clypeus and around ocellus (fig. 1). Male: lower portion of gena (fig. 8) and anterior portion of tegula with distinct yellow spot ..... *P. flavifrons* (Vachal, 1909)
- Female: lateral fovea of T2 narrow (fig. 24); head with fine and uniformly distributed punctures (fig. 3). Male: gena and tegula without yellow marks (figs. 4, 27) .....  
.....*P. punctata* (Urban, 2009)

#### *Psaenythisca flavifrons* (Vachal), new combination

*Psaenythia* (*Psaenythia*) *flavifrons* Vachal, 1909: 40. Holotype male, Argentina: Santa Fé, Las Garzas (MNHP, examined); Holmberg, 1921: 277; Moure et al., 2007: 49; Rasmussen, 2012: 28.

DIAGNOSIS AND COMMENTS: *Psaenythisca flavifrons* can be easily distinguished by the large yellow area on the face of male, with marks extending above the antennal socket and generally also present on the frons. Females can be recognized by the ellipsoid lateral fovea of T2, the large yellow area on the basal portion of tibia and the coarse punctures on the head, mainly on the clypeus and around the ocellus. In addition, males have a yellow spot on the lower portion

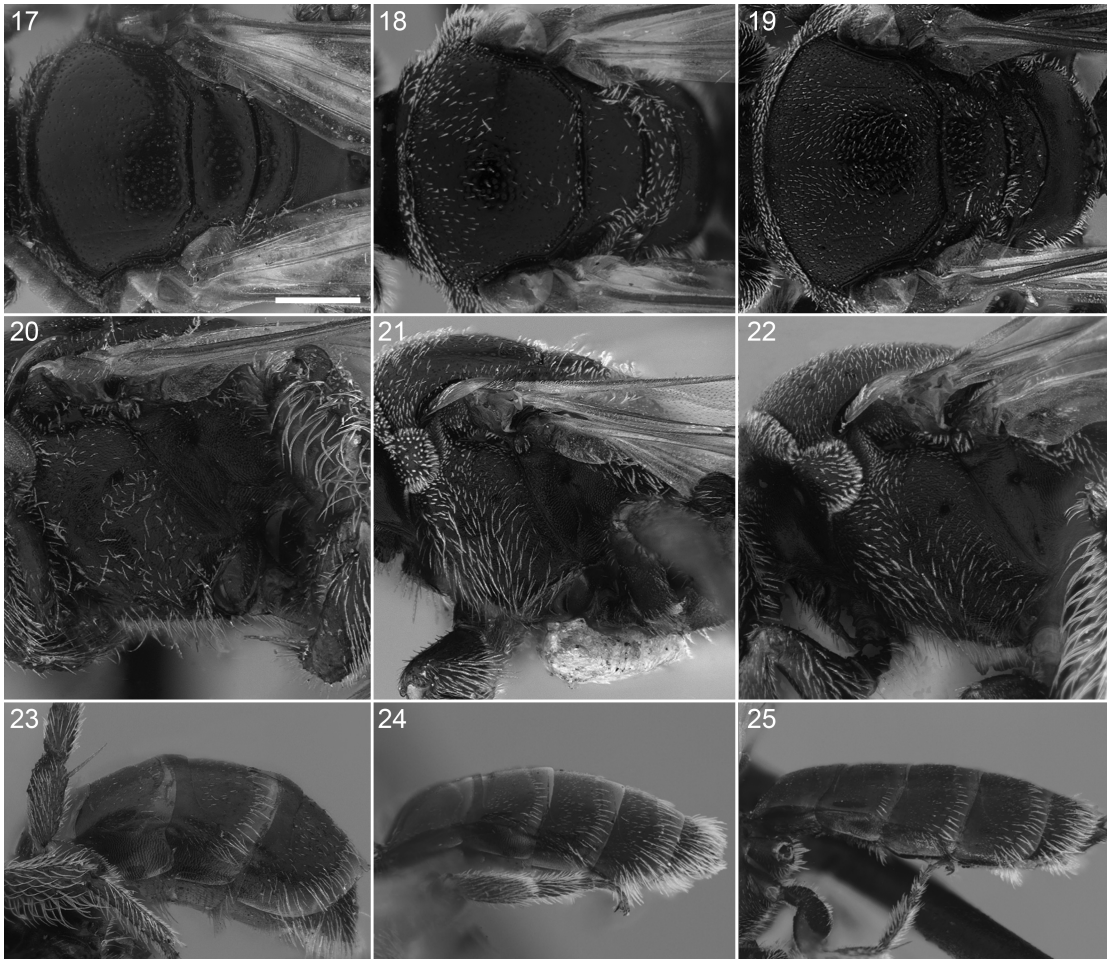




FIGURES 13–16. Males of *Psaenythisca*, new genus, with small head. **13.** *P. punctata* head in frontal view (from Villaguay). **14.** *P. punctata* lateral habitus (from Villaguay). **15.** *P. wagneri* (holotype) head in frontal view. **16.** *P. wagneri* (holotype) lateral habitus. Scale bars = 0.5 mm.

of the gena and the anterior portion of the tegula; the mandible is mostly yellow; the frons is strongly elevated with deep frontal line; mesoscutum, the head (mainly clypeus and supra-clypeal area) and metasomal sterna are smooth and shiny between punctures. The genitalia and associated sterna are shown in figures 42, 45, 49, 52, and 53.

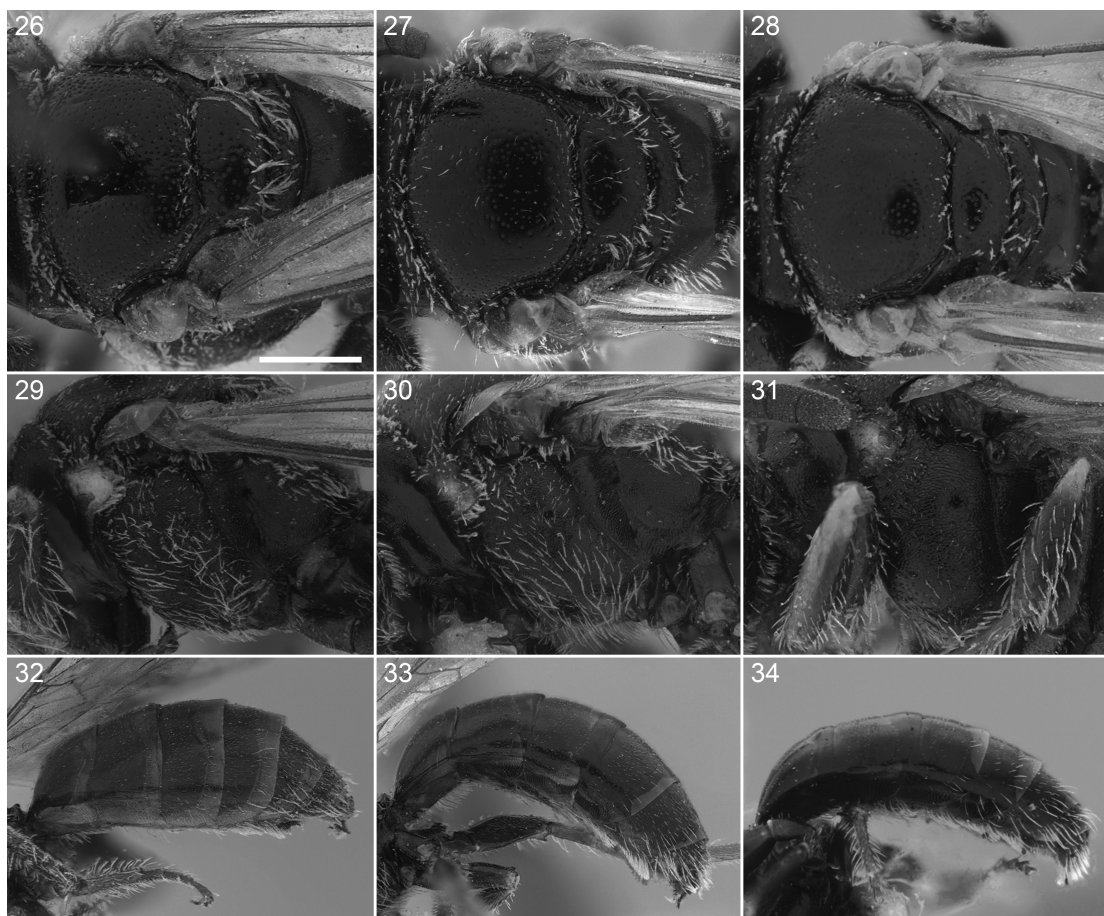
**REDESCRIPTION:** Holotype male (macrocephalic). Approximate body length: 4.2 mm; maximum head width: 1.7 mm; maximum mesoscutum width: 1.0 mm; forewing length: 3.1 mm; maximum width of T2: 1.5 mm. **Coloration.** Integument mostly brown, with following yellow parts: mandible (apex black), labrum, lower half of face, frons, lower portion of gena, pronotal lobe, small spot on anterior portion of tegula, apex of forefemur, large part of foretibia, basal two-thirds of mid- and hind tibia. Flagellum, anterior portion of scape, spurs, wing veins, and tarsus light brown; marginal zone of metasomal terga translucent brown. **Pubescence.** Head with sparse short hairs (0.3× as long as ocellus diameter); few longer hairs between ocelli (as long as diameter of ocellus); ventral portion of gena with sparse plumose pilosity. Pronotal collar and border of mesoscutum with dense short plumose hairs; disc of mesoscutum with



FIGURES 17–25. Females of *Psaenythisca*, new genus. 17–19. Mesosoma, dorsal view: 17. *P. flavifrons*, 18. *P. punctata*, 19. *P. wagneri*. 20–22. Mesepisternum, lateral view: 20. *P. flavifrons*, 21. *P. punctata*, 22. *P. wagneri*. 23–25. Metasoma, lateral view: 23. *P. flavifrons*, 24. *P. punctata*, 25. *P. wagneri*. Scale bar = 0.5 mm.

sparse, finely branched setae, their length about twice puncture diameter; scutellum, mesepisternum, and lateral corners of propodeum with dense long plumose hairs; metapostnotum with a few minute setae. Disc of metasomal terga with short finely branched setae on T1–T4; premarginal line with long branched hairs. *Integumental surface.* Head, mesoscutum, and scutellum predominantly smooth and shiny between punctures; lower portion of face, vertex, and gena smooth with sparse punctures ( $>3$  pd); frons and upper paraocular area with dense punctures (about 1 pd) and slightly reticulated between punctures. Pronotal collar and mesepisternum strongly reticulated; mesoscutum and metanotum densely punctate (about 2 pd) and smooth between punctures; metapostnotum reticulated with few fine longitudinal striations on middle portion. Metasoma most reticulated between punctures; disc of metasomal terga with fine, shallow, and sparse punctures (ca. 3 pd); marginal zone of metasomal terga shiny and slightly reticulated; metasomal sterna weakly reticulated on basal third; metasomal sterna densely punctate on distal half ( $\leq 1$  pd). *Structure* (measurements in mm). Head wider than

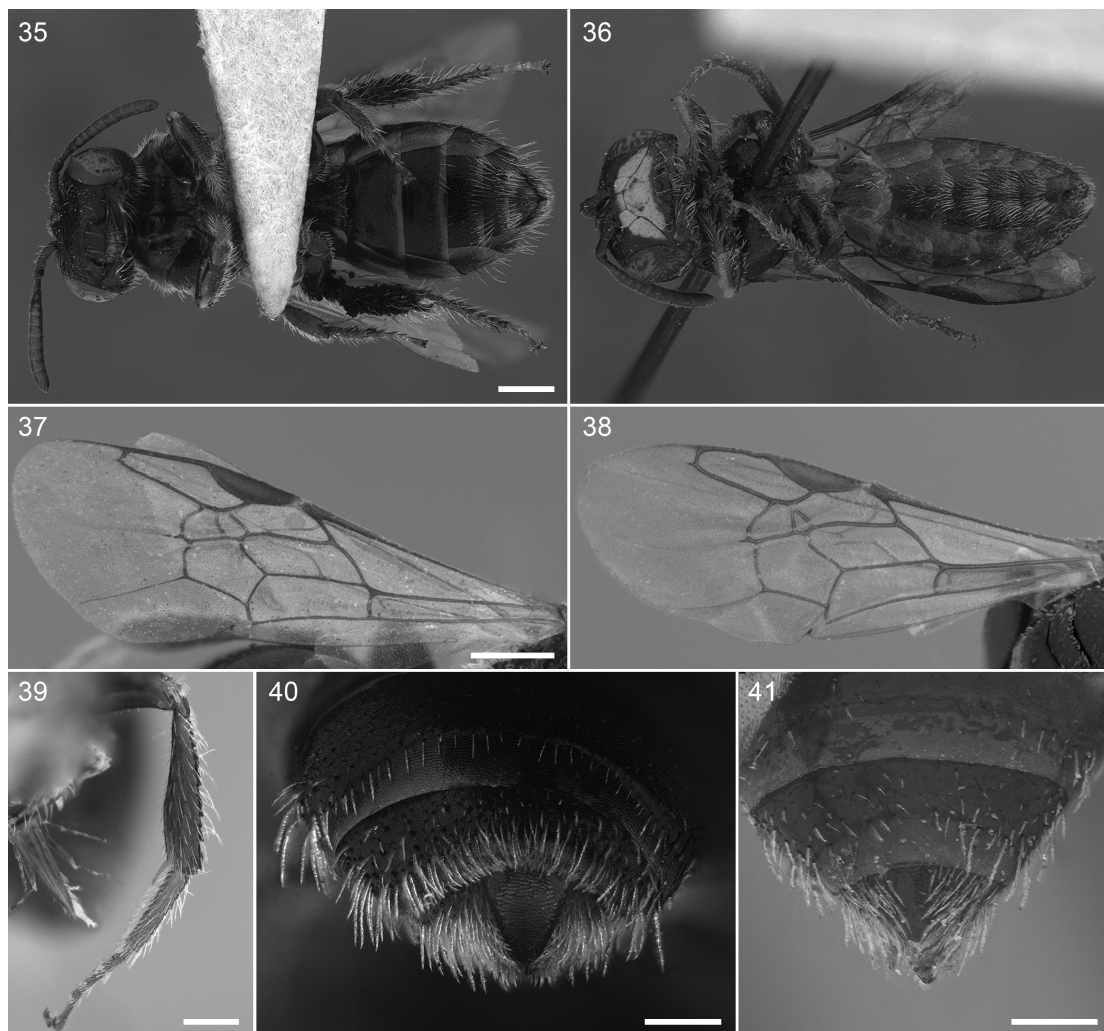




FIGURES 26–34. Males of *Psaenythisca*, new genus. Mesosoma, dorsal view: 26. *P. flavifrons*, 27. *P. punctata*, 28. *P. wagneri*. Mesepisternum, lateral view: 29. *P. flavifrons*, 30. *P. punctata*, 31. *P. wagneri*. Metasoma, lateral view: 32. *P. flavifrons*, 33. *P. punctata*, 34. *P. wagneri*. Scale bar = 0.5 mm.

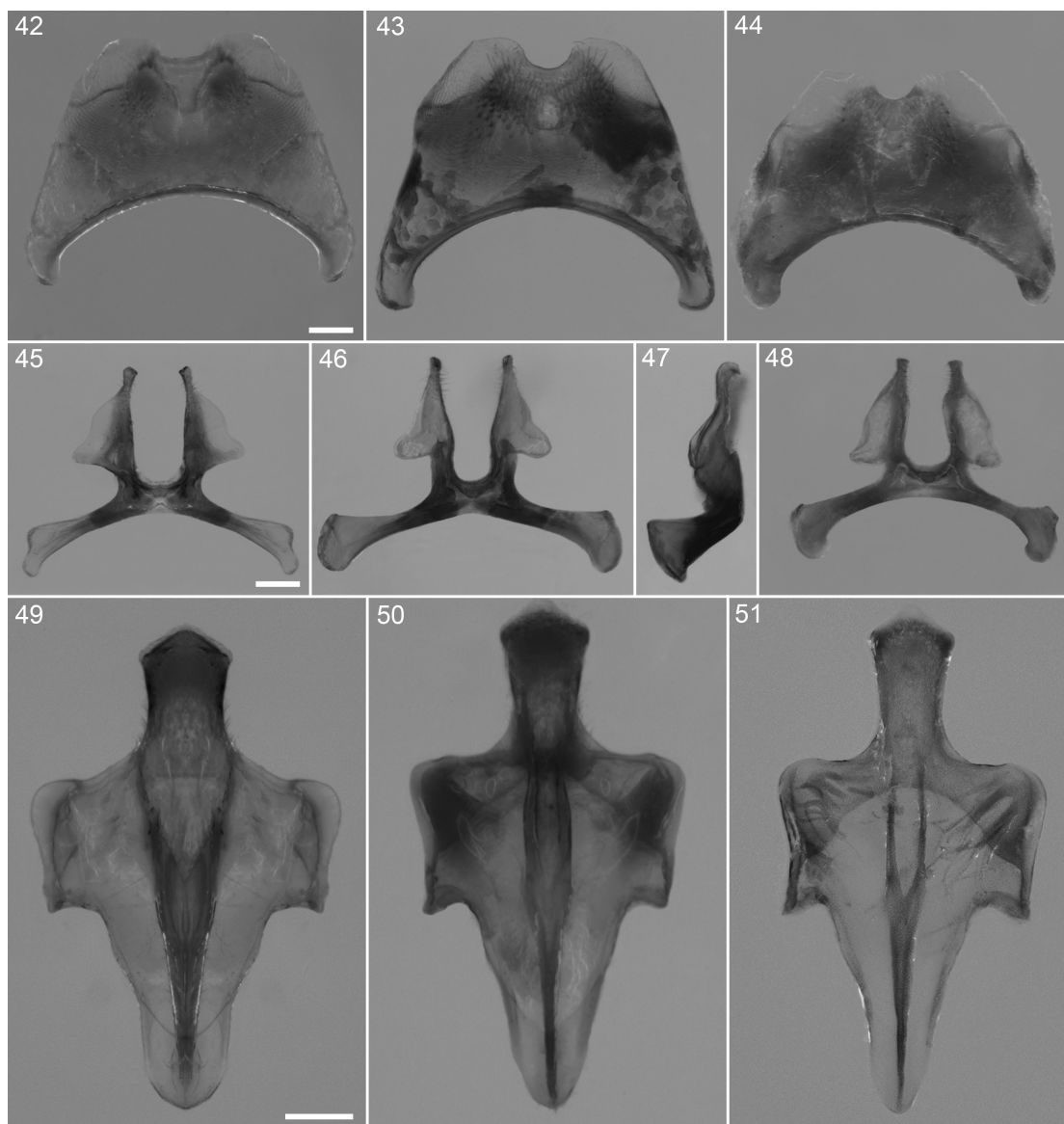
long (1.7:1.3); labral plate almost  $1.9\times$  wider than long (0.2:0.15); compound eyes about  $2\times$  longer than wide (0.8:0.4) and divergent below (upper to lower interorbital distance, 1.1:1.4); clypeus about  $4\times$  as wide as long (1.4:0.35); facial fovea almost  $2.4\times$  as long as wide (0.22:0.09); midtibial spur about  $0.8\times$  as long as basitarsus (0.27:0.33).

**DESCRIPTION:** Female. Approximate body length 4.8 mm; maximum head width 1.6 mm; maximum mesoscutum width 1.5 mm; forewing length 3.5 mm; maximum width of T2 1.6 mm. **Coloration.** Integument mostly dark brown with yellow area on basal portion of fore- and midtibia; posterior surface of flagellum light brown. **Pubescence.** Head with sparse and short hairs (about  $0.5\times$  as long as ocellar diameter). Pronotal collar and lobe with dense plumose pilosity; disc of mesoscutum, scutellum, and metanotum with minute sparse hairs; lateral borders of scutellum with longer branched pilosity; mesepisternum with finely branched hairs; metapostnotum with few minute setae on lateral portions; tibial scopae with sparse and long simple setae. Disc of T1–T2 with minute and very sparse hairs; subsequent terga with relatively long pilosity (on T2 about  $0.3\times$  as long than length of marginal zone); premarginal line of



FIGURES 35–41. 35. Female of *Psaenythisca punctata* in ventral view. 36. Male of *P. wagneri* in ventral view. 37. Male forewing of *P. punctata*. 38. Male forewing of *P. wagneri*. 39. Male hind leg of *P. punctata*. 40. Female pygidial plate of *P. wagneri*. 41. Male T7 of *P. wagneri*. Scale bars: figures 35–38 = 0.5 mm; figures 39–41 = 0.3 mm.

T3–T5 with sparse, long, and branched hairs; pygidial fimbria sparse. *Integumental surface.* Head predominantly smooth between punctures, with frons, upper paraocular area, and vertex reticulated between punctures; clypeus and lower paraocular area with sparse and shallow punctures; supraclypeal area and gena with dense punctation (about 0.5 pd); frons and around ocelli with dense and coarse punctation. Pronotum, mesepisternum, and propodeum reticulated; mesepisternum with very sparse and shallow punctures; mesoscutum and metanotum densely punctate ( $\leq 2$  pd), smooth between punctures; scutellum with sparse punctures (about 3 pd); metapostnotum reticulated with few fine longitudinal striations on middle portion. Metasoma slightly reticulated between punctures; disc of metasomal terga with very fine and sparse punctures ( $\geq 5$  pd); metasomal sterna with dense and coarse punctures on distal half



FIGURES 42–51. Male terminalia of *Psaenythisca*, n. gen., in ventral view (except figure 47). 42. S6 of *P. flavifrons* (from Otamendi). 43. S6 of *P. punctata* (from Villaguay). 44. S6 of *P. wagneri* (from San Pedro de Colalao). 45. S7 of *P. flavifrons*. 46. S7 of *P. punctata*. 47. S7 of *P. punctata*, lateral view. 48. S7 of *P. wagneri*. 49. S8 of *P. flavifrons*. 50. S8 of *P. punctata*. 51. S8 of *P. wagneri*. Scale bars = 0.2 mm.

(distance between punctures about 1 pd). *Structure* (measurements in mm). Head wider than long (1.63:1.26); labral plate almost 1.6× wider than long (0.33:0.2); eyes about 2× as long as wide (0.9:0.46) and almost subparallel (upper to lower interorbital distance, 1.1:1.08); clypeus about 2.5× as wide as long (1.0:0.4); facial fovea oval, almost 2.6× as long as wide (0.29:0.11); midtibial spur about 0.7× as long as basitarsus (0.35:0.46); pygidial plate hidden. Other complementary information on morphology as described for genus.





FIGURES 52–58. Male genital capsule of *Psaenythisca*, new genus. 52–53: *P. flavifrons* (from Otamendi), 52. ventral view, 53. dorsal view. 54–56: *P. punctata* (from Villaguay), 54. ventral view, 55. lateral view, 56. dorsal view. 57–58: *P. wagneri* (from San Pedro de Colalao), 57. ventral view, 58. dorsal view. Scale bars = 0.2 mm.



VARIATION: The yellow areas on frons, gena, and legs of males may slightly vary in size.

DISTRIBUTION: Argentina: Buenos Aires and Santa Fé (fig. 59).

TYPE MATERIAL EXAMINED: Holotype male (MNHP), "Museum Paris\ Chaco de Santa-Fé\ Las Garzas\ Bords du Rio Las Garzas\ 25 Kil. A L'O D'OCAMPO\ E. R. Wagner 1903" "Holotype"(red label) "Psaenythia\ flavifrons\ Vachal."

ADDITIONAL MATERIAL EXAMINED: **Argentina, Buenos Aires:** 1 ♀ and 2 ♂ (1 ♂ with terminalia dissected) (DZUP), "Ing. R. Otamendi\ Prov. Bs. Aires Arg.\ XI.1954 FH Walz."

*Psaenythisca punctata* (Urban, 2009), new combination

*Anthrenoides punctatus* Urban, 2009: 221. Holotype female, Argentina: Entre Rios, Villaguay (DZUP, examined).

DIAGNOSIS AND COMMENTS: *Psaenythisca punctata* can be recognized by the following combination of characters: narrow lateral fovea of T2 of females; dense and long pilosity around antennal socket and on the meso- and metasoma (especially in female); mandible, labrum, and clypeus of males yellow; gena of male and anterior portion of tegula without yellow spots; second submarginal cell of forewing with slightly convergent 1r-m and 2r-m; clypeus, paraocular, and supraclypeal area of female with smooth and shiny integument between punctures; mesoscutum and scutellum with sparse punctation ( $>2$  pd).

DESCRIPTION: Male (small head). Approximate body length: 4.6 mm; maximum head width 1.3 mm; maximum mesoscutum width 1 mm; forewing length 3 mm; maximum width of T2 1.4 mm. *Coloration.* Integument mostly brown, with following areas yellow: mandible (apex black), labrum, clypeus, lower paraocular area, supraclypeal area, subantennal areas, pronotal lobe, most of foreleg, articulation portion of femur with tibia, and hind basitarsus. Flagellum and wing veins brownish. *Pubescence.* Head with sparse and relatively long hairs (ca.  $0.5\times$  as long as ocellar diameter), with dense pilosity around antennal socket, few longer hairs between ocelli (as long as ocellar diameter), and ventral portion of gena with dense plumose pilosity. Pronotal collar, borders of pronotal lobe, and mesoscutum with dense short plumose hairs; disc of mesoscutum and scutellum with sparse, finely branched setae, their length about  $0.5\times$  the ocellar diameter; posterior border of scutellum and lateral corners of propodeum with long plumose hairs; upper half of mesepisternum with sparse and short hairs, their length gradually increasing toward ventral portion; metapostnotum with few minute setae. Disc of metasomal terga with short, finely branched setae with uniform length on T1–T4; premarginal line of T4–T6 with long, finely branched hairs. *Integumental surface.* Head, mesoscutum, and scutellum predominantly smooth and shiny between punctures; head with sparse punctures (ca. 3 pd); frons and around ocellus with dense punctures (about 1 pd) and slightly reticulated between punctures. Pronotal collar, mesepisternum, metapostnotum, and propodeum slightly reticulated; mesoscutum and metanotum with sparse punctures (about 3 pd); metapostnotum with few fine longitudinal striations on middle portion. Metasoma slightly reticulated between punctures; disc of metasomal terga with fine and sparse punctures ( $\geq 3$  pd); marginal zone of metasomal terga shiny and slightly reticulated. *Structure* (measurements in mm). Head wider

than long (1.3:1.1); labral plate almost 1.8× wider than long (0.28:0.15); eyes about 2× longer than wide (0.9: 0.48) and subparallel; clypeus about 3× as wide as long (1.0:0.3); facial fovea almost 2.3× as long as wide (0.26:0.11); midtibial spur about 0.6× as long as basitarsus (0.26:0.4). Genitalia and associated sterna as presented by figures 43, 46, 47, 50, 54, 55, and 56.

**VARIATION:** Few females from Villaguay and San Isidro (Argentina) have a longitudinal yellowish line on clypeus.

**DISTRIBUTION:** Argentina: Buenos Aires and Entre Rios (fig. 60).

**TYPE MATERIAL EXAMINED:** Holotype female (DZUP), "Prov. Entre Rios\ Villaguay Arg\ xi-20-1951\ Juan Foerster." Paratypes, **Argentina, Buenos Aires:** 1 ♀ (DZUP), "Campana B. Aires\ R.A. (F.N.G.B.M.)\ xii-1955 H. Walz." **Entre Rios:** 6 ♀ (DZUP), same data as holotype.

**ADDITIONAL MATERIAL EXAMINED:** **Argentina, Buenos Aires:** 2 ♀ (DZUP), "Hurlingham Prov.\ Buenos Aires Ar-\gentina, IV-50/ M.M. Senkute"; 1 ♀ (DZUP), "San Isidro, Prov.\ Buenos Aires Ar-\gentina IV-50/ M.M. Senkute"; 1 ♀ (MZSP), "San Isidro, Prov.\ Buenos Aires Ar-\gentina IV-50/ M.M. Senkute"; 1 ♀ (DZUP), "Prov. Buenos\ Aires, San\ Isidro, Arg.\ March 1-15.1954\ M.M. Senkute." **Entre Rios:** 3 ♀ and 5 ♂ (2 ♂ with terminalia dissected) (DZUP), "Prov. Entre Rios\ Villaguay Arg.\ XI-20-1951\ Juan Foerster"; 1 ♂ (MZSP) (with terminalia dissected), "Prov. Entre Rios\ Villaguay Arg.\ XI-20-1951\ Juan Foerster."

***Psaenythisca wagneri* (Vachal, 1909), new combination**

*Psaenythia* (*Psaenythia*) *wagneri* Vachal, 1909: 41. Lectotype male by present designation, Argentina: Santiago del Estero, Icaño (MNHP, examined); Holmberg, 1921: 277; Neff and Rozen, 1995: 14; Moure et al., 2007: 49; Rasmussen, 2012: 49.

**DIAGNOSIS AND COMMENTS:** *Psaenythisca wagneri* is distinct from the other two species by males with mandible and labral plate brownish, presence of reticulated integument on clypeus and paraocular and supraclypeal areas of females, and second submarginal cell of forewing with triangular shape, the veins 1r-m and 2r-m strongly convergent. Other important features for identification of *P. wagneri* are: yellow marks on lower paraocular area not extending to the margin of compound eyes; tegula without yellow spots; mesoscutum and scutellum of females with dense short hairs and punctures ( $\leq 1$  pd); basal portion of fore- and midtibia of females light brown. The genitalia and associated sterna as presented by figures 44, 48, 51, 57, and 58. This species seems to be associated with Malvaceae, with individuals of both sexes collected from flowers of *Sphaeralcea* sp. in Catamarca, La Rioja, and Salta provinces (Argentina).

**REDESCRIPTION:** Lectotype male (small head). Approximate body length: 4.0 mm; maximum head width: 1.23 mm; maximum mesoscutum width: 0.9 mm; forewing length: 2.7 mm; maximum width of T2: 1.2 mm. *Coloration.* Integument mostly brown, except following areas yellow: clypeus, supraclypeal area, subantennal area, pronotal lobe, most of foreleg, articulation region of tibia with femur of mid- and hind leg, hind basitarsus. Mandible (apex black), labrum, flagellum, wing veins, and tarsus light brown; tegula and marginal zones of metasoma translucent brown. *Pubescence.* Head with sparse and very short hairs; few longer hairs between ocelli (0.5 as long as ocellar diameter); ventral portion of gena with dense plumose hairs. Pronotal collar and border of mesoscutum and scutellum with sparse short plumose hairs; disc of mesoscutum

and scutellum with dense, finely branched and short (length about 2 pd) setae; metanotum and lateral corners of propodeum with dense, long, and plumose hairs. Disc of metasomal terga with short, finely branched setae (longer than 3 pd), uniform in length on T1–T5; premarginal line of T3–T6 with long, finely branched hairs, the length gradually increasing to T5. *Integumental surface*. Head, mesoscutum, and scutellum largely slightly reticulated between punctures; clypeus, paraocular, supraclypeal area, and vertex with sparse punctures ( $> 3$  pd); frons and gena with dense punctures (about 1 pd). Mesoscutum, scutellum, and metanotum slightly reticulated, with dense punctures (ca. 2 pd); mesepisternum, metapostnotum, and propodeum reticulated; metapostnotum with a few fine and very short longitudinal striations. Metasoma slightly reticulated between punctures; metasomal terga with finer sparse punctures (about 3 pd); marginal zone of metasomal terga shiny and slightly reticulated. *Structure* (measurements in mm). Head wider than long (1.23:1.0); labral plate almost 2 $\times$  wider than long (0.18:0.09); compound eyes about 2 $\times$  longer than wide (0.68:0.34) and slightly divergent below (upper to lower interorbital distance, 0.86:0.88); clypeus about 3 $\times$  as wide as long (0.9:0.3); facial fovea almost 2.8 $\times$  as long as wide (0.14:0.05); midtibial spur about 0.5 $\times$  as long as basitarsus (0.2:0.4).

**FEMALE.** Approximate body length 4.6 mm, maximum head width 1.43 mm, maximum mesoscutum width 1.14 mm, forewing length 3.5 mm, maximum width of T2: 1.42 mm. *Coloration*. Integument mostly black with mandible, flagellum, legs, and wing veins brownish; articulation of fore- and midfemur with tibia light brown. *Pubescence*. Head with dense and short hairs (about 0.5 $\times$  as long as ocellar diameter), shorter on vertex (about 2 pd). Pronotal collar and lobe with dense plumose pilosity; mesoscutum, scutellum, and metanotum with dense hairs, their length about 2 pd; posterior borders of scutellum and lateral corners of propodeum with longer plumose hairs; upper half of lateral mesepisternum with sparse and very short hairs (as long as diameter of punctures), gradually increasing in length on ventral portion; metapostnotum glabrous. Disc of metasomal terga with sparse and short hairs (minute on T1–T2); premarginal line of T2–T5 with sparse, longer plumose hairs; pygidial fimbria sparse. *Integumental surface*. Integument predominantly reticulated between punctures. Head with fine and dense punctures (ca. 2 pd), except clypeus with coarse punctures. Mesoscutum and scutellum slightly reticulated and shiny between punctures with dense punctures ( $\leq 1$  pd); mesepisternum with sparse (ca. 2 pd) and shallow punctures; metapostnotum with few very fine and short longitudinal striation. Metasoma slightly reticulated between punctures; disc of metasomal terga with sparse and very fine punctures ( $\geq 3$  pd), mainly on T1–T2; metasomal sterna with sparse punctures on distal half (about 2 pd). *Structure* (measurements in mm). Head wider than long (1.43:1.11); labral plate almost 1.6 $\times$  wider than long (0.3:0.18); compound eyes about 1.7 $\times$  as long as wide (0.8:0.46) and almost subparallel (upper to lower interorbital distance, 1.0:0.94); clypeus about 2 $\times$  as wide as long (0.74:0.37); facial fovea almost 2.4 $\times$  as long as wide (0.22:0.09); midtibial spur as long as basitarsus (0.4:0.46); tarsal claws bifid, with inner teeth reduced; pygidial plate V-shaped, with apex widely rounded.

**VARIATION:** The yellow areas present on clypeus of males may vary slightly in width (figs. 91, 92).

**DISTRIBUTION:** Argentina: Buenos Aires, Catamarca, La Rioja, Salta, Santiago del Estero, and Tucumán (fig. 61).

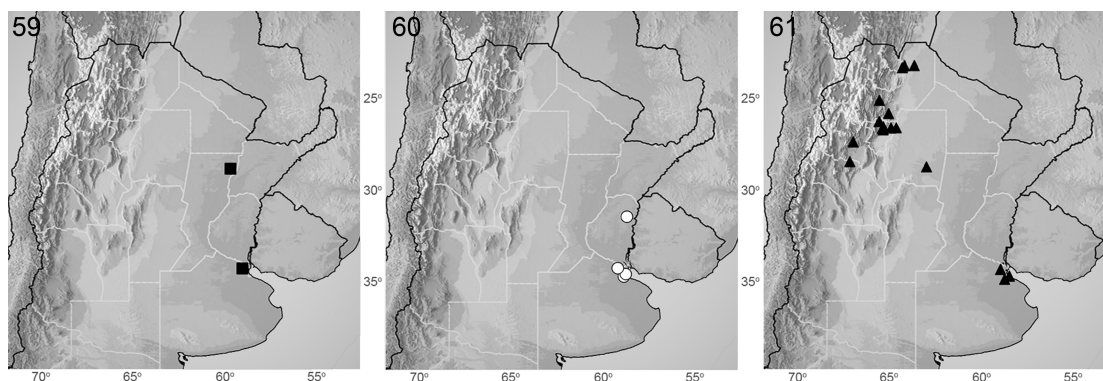
TYPE MATERIAL EXAMINED: Lectotype male (MNHP), "Museum Paris\ Chaco del Santiago del Estero\ Bords du Rio Salado\ env. D'Icaño\ E.-R. Wagner 1904" "Holotype"(red label) "Psaenythia\ wagneri\ Vachal." Paralectotype male (DZUP), same data as lectotype.

ADDITIONAL MATERIAL EXAMINED: **Argentina, Buenos Aires:** 6 ♀ (on two pins) (DZUP), "C. Federal R. A.\ B. Aires 21-II/1955 F. Walz"; 3 ♀ and 4 ♂ (2 males with terminalia dissected) (DZUP), "Ing. R. Otamendi\ Prov. Bs. Aires Arg.\ XI.1954 FH Walz"; 1 ♂ (DZUP), "Gonzales Catan.\ Buenos Aires,\ Argentina II-1952\ Juan Foerster." **Catamarca:** 1 ♀ and 1 ♂ (AMNH), "Argentina, Catamarca:\ San Fernando\ November 25, 1989\ J.G. Rozen and A. Roig"; 2 ♀ and 1 ♂ (AMNH), "Argentina, Catamarca:\ San Fernando\ Nov. 30-Dec. 1, 1989\ J.G. Rozen and A. Roig"; 6 ♀ and 8 ♂ (AMNH), "Argentina, Catamarca:\ San Fernando\ March 7, 1990\ J.G. Rozen and A. Roig"; 3 ♀ and 5 ♂ (AMNH), "Argentina, Catamarca:\ San Fernando\ March 7, 1990\ J.G. Rozen and A. Roig\ on *Sphaeralcea*." **La Rioja:** 39 ♀ and 19 ♂ (AMNH), "Argentina, La Rioja:\ San Blas Nov.12, 1991\ J.G. Rozen, L. Pena and\ A. Ugarte on\ *Sphaeralcea*." **Salta:** 1 ♀ (AMNH), "Argentina, Salta:\ 10 km S El Carril\ November 11, 1989\ J.G. Rozen and A. Roig"; 2 ♀ and 1 ♂ (AMNH), "Argentina, Salta:\ 10 km S El Carril\ November 11, 1989\ J.G. Rozen and A. Roig\ on *Sphaeralcea*"; 5 ♀ and 1 ♂ (AMNH), "Argentina, Salta:\ 6 km E Embarcación\ November 16, 1989\ J.G. Rozen and A. Roig"; 37 ♀ and 3 ♂ (AMNH), "Argentina, Salta:\ 40 km WNW Hickmann\ November 12-14, 1989\ J.G. Rozen and A. Roig"; 1 ♀ (AMNH), "Argentina\ Salta: 6km SW Pichanal\ XI-11-1993 JG and BL Rozen"; 3 ♂ (AMNH), "Argentina, Salta:\ 59km SSW Rosario de\ la Frontera\ Nov. 8, 1991\ J.G. Rozen, L. Pena\ and A. Ugarte." **Santiago del Estero:** 1 ♂ (DZUP), "Museum Paris\ Chaco de Santiago del Estero\ Bordo du Rio Salado\ Env. D'Icaño\ E. R. Wagner 1904." **Tucumán:** 1 ♀ (AMNH), "Argentina, Tucumán:\ 11km N Cadillal,\ March 3, 1990\ J.G. Rozen, L. Pena\ and A. Ugarte"; 1 ♀ (AMNH), "Argentina, Tucumán:\ 11km N Cadillal\ November 7, 1991\ J.G. Rozen, L. Pena\ and A. Ugarte"; 1 ♀ (AMNH), "Argentina, Tucumán:\ 12 km N El Cadillal\ November 8-9, 1989\ J.G. Rozen and A. Roig"; 1 ♂ (AMNH), "Argentina, Tucumán:\ 11km NW El Cadillal\ Nov. 7, 1991\ J.G. Rozen, L. Pena\ and A. Ugarte"; 1 ♀ (AMNH), "Argentina, Tucumán:\ between Las Cejas and\ Gobernador Garmendia\ October 29, 1989\ J.G. Rozen and A. Roig"; 1 ♀ (IMLA), "Argentina, Pr. Tucuman\ S.P. de Colalao\ collector J.L. Neff\ 2-II-74"; 1 ♀ and 1 ♂ (DZUP), "Argentina, Pr. Tucuman\ S.P. de Colalao\ collector J.L. Neff\ 2-II-74"; 1 ♀ and 2 ♂ (MZSP) (with terminalia dissected), "Argentina, Pr. Tucuman\ S.P. de Colalao\ collector J.L. Neff\ 2-II-74"; 1 ♀ and 7 ♂ (AMNH), "Argentina, Tucumán:\ between Taruca Pampa and\ Rio del Nio\ October 29, 1989\ J.G. Rozen and A. Roig"; 7 ♀ and 1 ♂ (AMNH), "Argentina, Tucumán:\ Tapia Nov. 21, 1989\ J.G. Rozen and A. Roig"; 8 ♀ and 1 ♂ (AMNH), "Argentina, Tucumán:\ 8 km SW Ticucho,\ March 24, 1990\ J.G. Rozen and A. Roig"; 1 ♀ (AMNH), "Argentina, Tucumán:\ 8 km SW Ticucho,\ March 25, 1990\ J.G. Rozen and A. Roig."

## NESTING BIOLOGY AND IMMATURES OF *PSAENYTHISCA WAGNERI* (VACHAL)

### NESTING BIOLOGY

While on a field trip together, Arturo Roig-Alsina and J.G.R. discovered a single nest entrance of *Psaenythisca wagneri* on partly shaded, level ground at 40 km WNW of Hickmann,



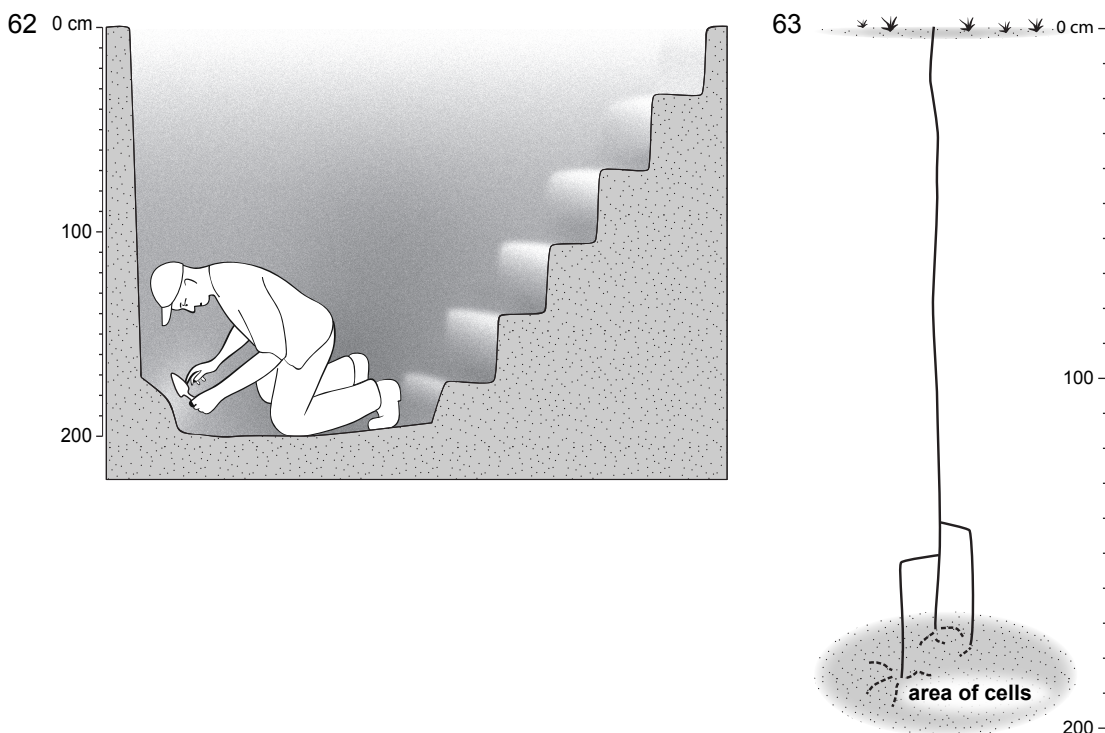
FIGURES 59–61. Maps of Northern Argentina showing the distribution of the species of *Psaenythisca* Ramos, new genus. 59. *P. flavifrons*. 60. *P. punctata*. 61. *P. wagneri*.

Salta Province, Argentina, on November 13, 1989. J.G.R. took extensive notes, presented here: When first discovered there was no reason to believe that such a small bee, 4.0–5.5 mm long, would have a nest nearly 2 m deep and that it would take two days to excavate. J.G.R. began by digging a shallow but moderately wide hole about 10 cm from it to receive excavated soil as he slowly removed the ground between the hole and the tunnel, starting at the surface and working down. Tools used were shovel, trowel, penknife, and an aspirator for blowing away loose soil from tunnel and cells. He occasionally blew white powder (plaster-of-Paris) from a plastic applicator bottle to highlight the tunnel. As the tunnel was revealed, it was necessary to enlarge and deepen the hole next to it so that he could fit into it and bend over to observe tunnel and cells as they were uncovered. As the hole deepened, he eventually needed to build steps to the rear so that he could climb out of it. When he reached the cells, J.G.R. frequently used the stairs to access the microscope above to examine cell fragments and contents. By that time, the hole with him in it looked approximately as diagramed in figure 62. Since the soil was quite dry and compact, it was unnecessary to brace the walls to avoid their collapsing, but, in other circumstances, this would have been prudent.

The soil below was fine-grained, hard, dry and contained only a few fine roots. On the first day, the open, nearly vertical main tunnel, 2.0–3.0 mm in diameter, was followed down 112 cm without a single cell being encountered. On the following day after further excavation, the tunnel was found to branch at the depth of 140 cm, yielding a tunnel that extended sideways for about 6 cm before becoming vertical and dropping to a depth of 170 cm. There it turned and abruptly connected to a closed horizontal cell containing a pupa. The main tunnel continued its vertical descent and branched again at 150 cm, with that branch again becoming vertical 6 cm from the main tunnel.

As indicated in figure 63, numerous cells were found 170–185 cm in depth and others may well have occurred farther below. In the vicinity of the cell area, the soil was compacted, and burrows were numerous and extended in many directions. Arranged singly, all cells were horizontal or tipped at most 10° toward the rear. Cell lengths were 5.3–6.0 mm ( $N = 4$ ) and maximum diameters were 3.0–3.2 mm ( $N = 5$ ). In general shape, the cell was broadly rounded at





FIGURES 62, 63. Diagrams of excavation to study the nest of *Psanythisca wagneri* and of the nest itself, to different scales, respectively; for explanation see Methods and Terminology.

the posterior end and narrowed evenly to the closure end (fig. 64). The inner surface of the closure, 2.0 mm in diameter, was a shallowly concave spiral consisting of about 4 coils (fig. 65). Cell walls (fig. 66) were extremely smooth, partly owing to the fine soil texture, but also almost certainly because they had a water-retardant lining, clearly indicated by water droplets that were only slowly absorbed both at the time of excavation and 24 years later (fig. 67).<sup>3</sup> The wall itself was more consolidated than the surrounding soil, suggesting that it has been modified by the female in the process of being constructed. However, the color of the wall was the same as the surrounding soil.

Food masses were flattened spheres with a maximum horizontal diameter of 2.3–2.35 mm ( $N = 4$ ) and height 1.9–2.15 ( $N = 3$ ); their top surfaces were slightly broader and flatter than their bottom surfaces. They were positioned toward the round rear of the cell leaving most of the cell floor in front of them (fig. 64). Several food spheres appeared to have a very thin outer coating that may, or may not, cover all of the provisions but floated off the provisions when they were submerged in water.

<sup>3</sup> It is noteworthy that the material (possibly in combination with construction technique) regulating humidity in the brood cell does not degrade over a 24-year period. This also demonstrates the value of storing nest components in museum collections for future evaluation.





FIGURES 64–69. Nest cells of *Psaenythisca wagneri*. **64.** View of cell from above, demonstrating broad cell rear and gradually narrowing toward front end (to right); sand (accident resulting from excavation) covered provision mass at rear of cell. **65.** Spiral cell closure, inside view. **66.** Same as figure 65 but focused on cross section of cell wall showing smooth texture compared with surrounding soil. **67.** Cell wall being tested with water droplet (arrow) demonstrating degree of permeability for water. **68, 69.** Feces at posterior ends of two cells.

Eggs rested on the top surface of the provisions in the median sagittal plane of the cell. They are described in the section on Immature Stages.

Small larvae ate the provisions beneath their heads, and intermediate stage larvae continued to do so, without moving from where their eggs had been deposited. Large larvae did not reorient themselves as do those of *Calliopsini*. They remained facing cell closures until they finished eating and thus were not found on their dorsa while feeding on provisions held on their venters. However, fully fed, predefecating larvae were found on their dorsa. Preserved cells show that feces are deposited at the rear of the cell either in the form of elongate pellets (fig. 68) or as somewhat smeared streaks (fig. 69).

Many individuals of all life stages (eggs, larvae, pupae, as well as adults) were recovered at the time of our excavation, except inactive postdefecating larvae were not encountered, indicating that this bee was multivoltine and did not undergo diapause at the time of the year when the site was discovered. More than 20 females were within the nest, of which 12 were preserved, as were 52 mature larvae, of which 18 were postdefecating forms (fig. 71). Two eggs and 18 small immature larvae were recovered. Of 37 pupae, 23 were females (fig. 74) and 14 males. Whereas all females were uniform in size, 5 males were small bodied with normal, small heads and mandibles, but the 9 other pupae had heads somewhat to greatly enlarged (fig. 76), with mandibles that were also vastly enlarged; bodies of these tended to be larger than those with small heads.

An unexplained phenomenon regarding pupae is that among all that were there, not one was preserved that had its adult integument pigmented. At most, some males and females had eyes that had become reddish and in some of these mandibles had taken on a hint of adult color, but none had body color. Might this suggest that pigmentation is a very quick phase of pupal development and/or that pupal development is staggered, so that new adults emerge more or less simultaneously? An unfortunate consequence of this phenomenon is that it is impossible to relate the numerous pupal tubercles to adult setae or structures that the tubercles might accommodate.

No active adult males were found in the nest or in the immediate vicinity of the nest. However, they were observed around the flowers of *Sphaeralcea* (Malvaceae), the food source for this species, which grew within 3 m of the nest. Likely that is where mating took place.

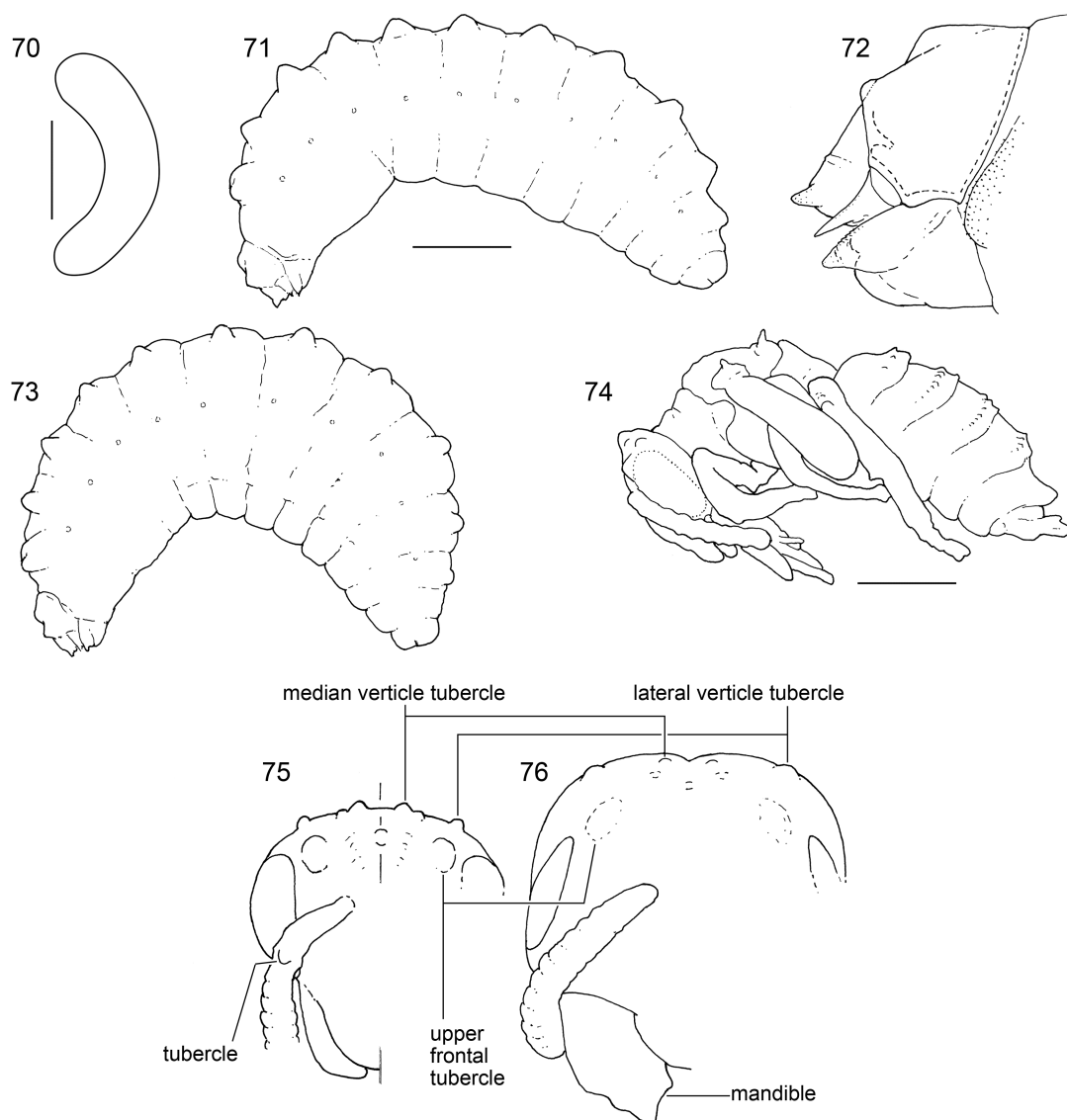
#### IMMATURE STAGES

The mature larva and pupa, though not described before, were compared with those of other panurgines by Neff and Rozen (1995) as "*Anthrenoides* species near *wagneri* (Vachal)." Specimens examined were those collected at 40 km WNW of Hickmann, Salta Province, Argentina, on November 13, 1989.

#### EGG

##### Figures 70, 81, 82

White eggs with reflective, transparent chorions were relatively stout. One, measured when discovered, had a maximum diameter of 0.375 mm near the front end and a length of 1.2 mm, while its median diameter was 0.325 mm. A preserved egg measured 24 years later had a maxi-



FIGURES 70–76. Diagrams of immatures of *Psaenythisca wagneri*. 70. Egg, lateral view. 71. Postdefecating larva, lateral view. 72. Head of same, lateral view. 73. Predefecating larva, lateral view, to same scale as fig. 71. 74. Female pupa, lateral view. 75. Head of female pupa, frontal view. 76. Head of macrocephalic male pupa, frontal view.

mum diameter of 0.30 mm, a maximum length of 1.1 mm, and a median diameter of 2.75 mm. A mature oocyte from a preserved female had a maximum diameter of 0.30 mm and a maximum length of 1.1 mm. All were strongly curved with their maximum diameters just behind their anterior ends and tapered moderately from their rounded front ends most of the way toward the rear ends, which were also rounded but smaller than the front ends (fig. 70). The micropyle, at the anterior end of the egg, consisted of a transverse cluster of openings with little chorionic sculpturing that was visible only with an SEM (figs. 81, 82).

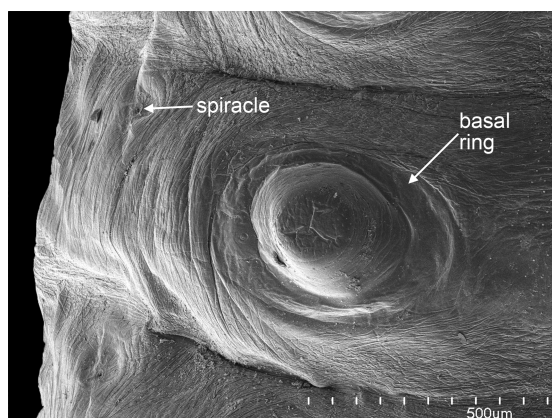


FIGURE 77. SEM micrograph of left side of abdominal segment 3, dorsal view, showing paired dorsal tubercle with sclerotized ring at base.

The single female dissected bore one mature oocyte, and almost certainly had an ovarian formula of 3:3, i.e., three ovarioles per ovary.

#### MATURE LARVA

Figures 71–73, 77–80, 83–90

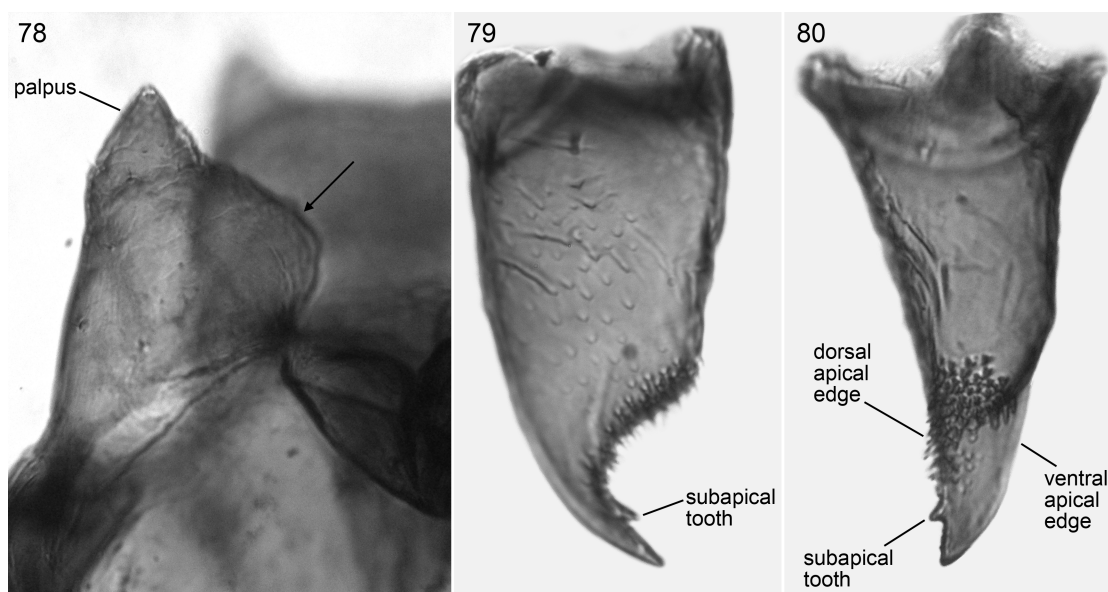
**DIAGNOSIS:** The mature larva of *Psaenythisca wagneri* agrees closely with those of other Protandrenini described to date: *Pterosarus boylei* (Cockerell) (described as *Pseudopanurgus boylei* in Rozen, 1966); *Pterosarus occiduus* Timberlake (described as *Pseudopanurgus* species A in Rozen, 1966); *Pseudopanurgus aethiops* (Cresson) (Rozen, 1966); *Pseudopanurgus verticalis* Timberlake (described as *Pseudopanurgus* species B in Rozen, 1966); *Protandrena verbesinae* (Timberlake) (described as *Psaenythia bicolor* Timberlake in Rozen, 1970); *Anthemurgus passiflorae* Robertson (Neff and Rozen, 1995); and *Parasarus atacamensis* Ruz (Ruz and Rozen, 1993). Although among these taxa there is some variation in the degree of development of the antennal prominences and configuration of the shape of the lateral profile of the upper frons and vertex, protandrenine larvae are a homogeneous group.

The following description is based on mature pre- and postdefecating larvae collected at 40 km WNW of Hickmann in 1989. All postdefecating specimens were actively developing into pupae, i.e., none were quiescent.

**DESCRIPTION: Head:** Integument with scattered, minute sensilla, some of which are finely setiform; entire lower border of clypeus with dense patch of transverse linear rows of minute, sharp-pointed spicules, visible with SEM (figs. 84, 85); dorsal surfaces of maxilla and upper part of hypopharynx densely spiculate (fig. 83); epipharynx spiculate sublaterally. Integument unpigmented except mandibular apices and to lesser extent hypostomal and pleurostomal ridges at most moderately pigmented.

Head size (figs. 71, 82) of postdefecating larva moderate compared with body size. Tentorium of predefecating larva complete, including dorsal arms, but not robust. Anterior tentorial pit close to anterior mandibular articulation in frontal view (fig. 83); postoccipital, hypostomal, and pleurostomal ridges well developed but moderately thin; dorsal ramus of hypostomal ridge absent; epistomal ridge laterad of (below) anterior tentorial pit short; internal ridge between pits absent; median longitudinal thickening of head capsule (coronal ridge) absent. Parietal bands not evident on clear head capsule but slightly indicated on SEM (fig. 83). Antennal prominence moderately developed (fig. 83); antennal disc as seen on cleared specimen large, its diameter somewhat greater than distance from its outer rim to center of anterior tentorial pit (fig. 83); antennal papilla large, unpigmented, domelike, projecting about one-half basal diameter (fig. 83), bearing three sensilla. Clypeus immediately above labrum with band of transverse rows of fine spicules (figs. 85, 86). Upper part of head in lateral profile distinctly



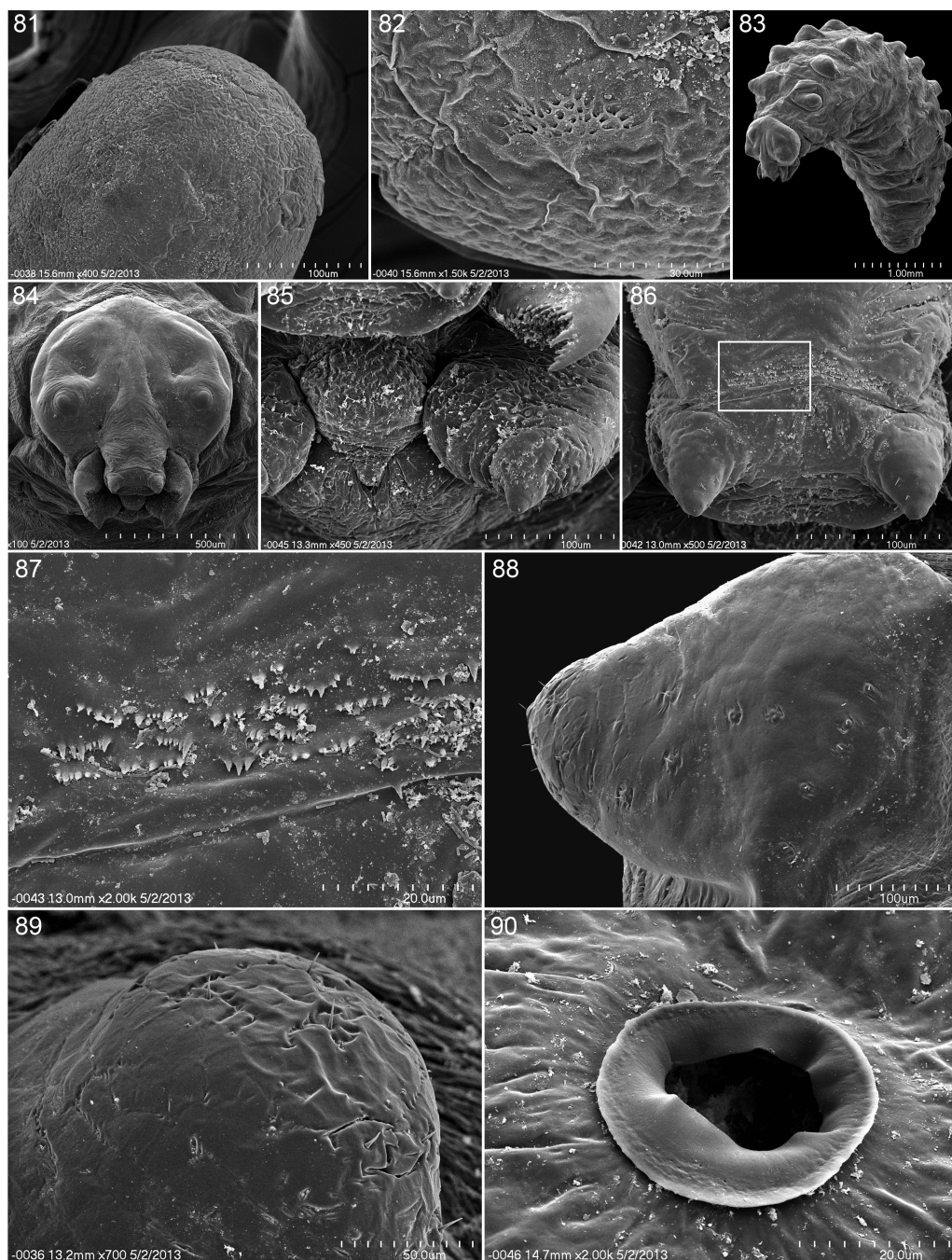


FIGURES 78–80. Microphotographs of mature larva of *Psaenythisca wagneri*. **78.** Right maxilla with mandible removed and labrum behind, ventral view, showing maxillary palpi and strongly developed adoral surfaces (arrow). **79, 80.** Right mandible, dorsal and inner views, respectively, showing spiculate dorsal surface and teeth along dorsal apical edge including enlarged subapical tooth and smooth ventral apical edge.

angled between vertex and frons as in figure 72. Labrum projecting farther than lower edge of clypeus in lateral view (fig. 72).

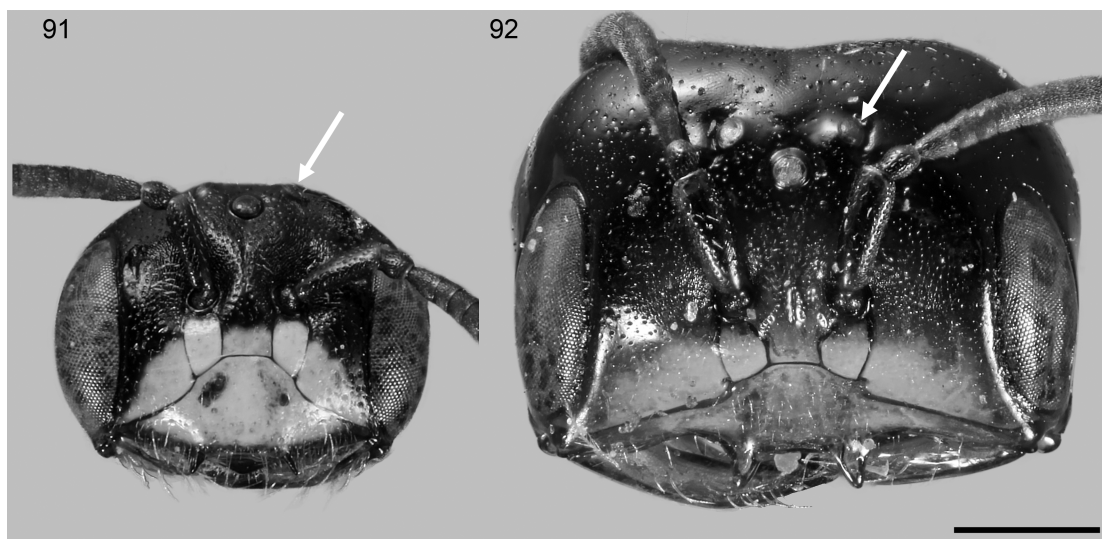
Mandible (figs. 78, 79) with large subapical tooth in addition to long dorsal row of smaller, sharply pointed teeth that broadens basally to become broad multidentate cusp; ventral apical edge smooth; dorsal surface of mandible broadly, sparsely spiculate. Maxilla strongly projecting in lateral view (fig. 72), but labium recessed; apex of maxilla projecting but not as far as apex of labrum in lateral view (fig. 72); cardo evident as sclerite; stipes evident only with staining; articulating arm of stipital sclerite not evident, although hypopharyngeal groove extremely deep because of bulging hypopharynx above and bulging labial apex below; maxillary apex broad because of strong development along adoral side, with result that large, conical palpus arises from aboral side (fig. 85). Labial pre- and postmentum weakly distinguishable (premental sclerite not evident); labial apex strongly bilobed, each lobe serving as base to small palpus. Labial lobes separated by small, recessed (relative to labial lobes), median salivary lobe, around which is salivary opening. Hypopharynx protuberant, projecting forward somewhat farther than labial apex in lateral view (fig. 72); hypopharyngeal groove strongly defined because of protuberant surrounding surfaces.

**Body** (figs. 71, 73, 77): Integumental vestiture consisting of minute, widely distributed spicules and very fine setiform sensilla; only lateral pronotal lobes immediately posterior to posterior tentorial pits conspicuously spiculate; paired dorsal body tubercles lacking setae visible by stereoscope, but with minute setiform sensilla clearly visible with SEM (figs. 88, 89); these tubercles weakly but distinctly sclerotized with extreme apices finely roughened, best seen with SEM (figs.



FIGURES 81–90. SEM micrographs of immatures of *Psaenythisca wagneri*. **81.** Front end of egg, showing position of micropyle. **82.** Another view of micropyle, close-up. **83.** Entire postdefecating larva, frontal lateral view. **84.** Head of same, frontal view. **85.** Mouthparts, frontal view. **86.** Clypeal apex and labrum. **87.** Close-up of transverse rows of minute spicules along clypeal apex identified by rectangle in figure 86. **88, 89.** Right prothoracic and left metathoracic tubercles, respectively, showing setiform sensilla. **90.** Spiracle, external view.





FIGURES 91, 92. Macrophotographs of male heads of *Psaenythisca wagneri*, same scale, frontal view, demonstrating differences in size and shape between small-headed and large-headed individuals.

77, 88, 89); base of tubercles of midbody segments surrounded by sclerotized ring (fig. 77), but rest of dorsal body surface membranous. Body form of predefecating larva robust (fig. 73); that of postdefecating larva obviously more linear (fig. 71); intersegmental lines moderately weakly incised on postdefecating and predefecating larvae (figs. 71, 73); dorsal intrasegmental lines not evident; paired dorsal tubercles present on all body segments except abdominal segments 9 and 10 of predefecating and postdefecating larvae; paired dorsal tubercles of prothorax with apices more lateral in position than those of other body segments, giving entire tubercles a more transverse appearance; all other tubercles uniform in having rounded apices, each approximately half as high as basal diameter, with sizes diminishing beyond abdominal segment 6; abdominal segment 9 not produced ventrally; abdominal segment 10 positioned medially on 9 as seen in lateral view (figs. 71, 73); anus apical on 10; as seen in lateral view, area above anus somewhat larger than area below, terminating as simple curved surface (i.e., not projecting upward and not bilobed). Spiracles (figs. 71, 73) difficult to detect because weak sclerotization and small size except on cleared specimens; first pair on thorax moderately small and those of following segments decreasing in size, so that those of abdominal segment 8 with diameter of atrium about one-half that of first thoracic pair; distinct rim and peritreme present (fig. 90); subatrium with 6 or 7 chambers, primary tracheal opening with collar. Sex recognition characters unknown.

#### FEMALE PUPA

Figures 74, 75

The female is described first because its form is less variable than that of the male, and it can serve as a basic plan for male anatomy. The format follows that of Yager and Rozen (1966), and the terminology for dorsal head tubercles is that of Neff and Rozen (1995: fig. 20).

**DIAGNOSIS:** To date, protandrenine pupae of only *Anthemurgus passiflorae* Robertson (Neff and Rozen, 1995) and *Protandrena verbesinae* (Timberlake) (as *Psaenythia bicolor* Timberlake, Rozen, 1970) have been characterized. The pupae of these two taxa and of *Psaenythisca wagneri* uniquely display dorsal head tubercles unlike those seen on other panurgine pupae.<sup>4</sup> Thus, the combination of paired median and lateral vertical tubercles and paired upper frontal tubercles, in addition to ocellar tubercles, may turn out to be a synapomorphy of the tribe.<sup>5</sup> The pupa of *Neffapis longilingua* has also been described (Rozen and Ruz, 1995), but it lacks the full display of head tubercles, supporting the removal of the genus from the tribe (Engel, 2005: 14, based on Ascher, 2004).

**DESCRIPTION:** Length corresponding to that of adults. **Head:** Pedicel with small rounded tubercle on outer surface. Ventral surface of mandible without tubercle near base. Vertex and upper part of frons with paired median vertical tubercles close to lateral ocellar tubercles; lateral vertical tubercles only slightly larger than median vertical tubercles; median ocellus lacking distinct tubercle; upper frontal tubercle large, dome shaped; area between upper frontal tubercles verrucose; gena with small tubercles.

**Mesosoma:** Lateral angles and posterior lobes of pronotum not produced; mesoscutum without tubercles, indistinctly verrucose; mesoscutellum with pair of projecting tubercles; axillae not swollen; metanotum swollen medially, indistinctly bilobed; mesepisternum without tubercle. Tegula with small, distinct tubercle. Outer surface of base of forewing uneven, swollen, but without tubercle. Each coxa with apical tubercles; foretrochanter with apical tubercle; base of hind tibia with moderately small rounded tubercle on outer surface and apex with small rounded spiculate tubercle on outer surface in addition to pair of tubercles accommodating adult spurs on inner surface.

**Metasoma:** Terga 1–5 each with subapical row of low, small, apically blunt tubercles. Terminal spine short, apically rounded.

#### MALE PUPA

##### Figure 76

**DESCRIPTION:** As described for female except terga 1–6 each with subapical row of low, small, apically blunt tubercles.

**REMARKS:** As mentioned in Nesting Biology (above), male pupae have heads that are proportional to their body size or heads that are more or less substantially enlarged compared with body size. The former tend to be smaller than the females, but tubercles on the

<sup>4</sup> After writing this statement, J.G.R. recovered two pupa (male and female) identified as *Psaenythia* “black,” collected as larvae from the same nest at San Fernando, Catamarca Province, Argentina, November 4, 1989, by J.G. R., reared and preserved as pupae on Nov. 26. Another specimen from that nest was preserved on November 15 as a postdefecating larva. The dorsal pupal head tubercles were easily recognized, though with some modification in size, and found to be those of the other three protandrenine genera, bringing the total to four. Both male and female also bore a tubercle on the antennal pedicel.

<sup>5</sup> Dorsal head tubercles and spines have also been reported on pupae of *Perdita* (Michener and Ordway, 1963; Yager and Rozen, 1966; Torchio, 1975; Eickwort, 1977). Their distributions and fewer numbers do not seem to correspond with those of known protandrenine pupae and may be functionally associated with a single elongate terminal spine not found in the Protandrenini. They are, therefore, not thought to be homologous with the dorsal head tubercles of the latter.

vertex and frons are substantially the same as those of females, identified in the description of the female pupa above and in figure 75. The large-headed (macrocephalic) male pupae have the same dorsal head tubercles as the female but modified in size and slightly in position; their body size is about the same as that of the females. Their lateral vertical tubercles are smaller and more widely separated (fig. 76); the median vertical tubercles are slightly forward relative to the lateral tubercles, and the lateral ocellar tubercles are decreased in size, so that they are visible merely as an integumental scar well forward of, and separated from, the median vertical tubercles. The upper frontal tubercles are less pronounced, although approximately in the same position.

MATERIAL STUDIED: All pupae from one nest as identified under Nesting Biology (above).

#### DISCUSSION: NESTING BIOLOGY AND IMMATURES OF *PSAENYTHISCA WAGNERI* (VACHAL)

Although this study gives us some insight into the nesting biology of this species and therefore into the genus, it also raises questions that need further investigation:

Panurgines tend to nest shallowly, and species of most Protandrenini have nests less than 50 cm deep (Rozen, 1989; Neff and Rozen, 1995) in contrast of the nest of *Psaenythisca wagneri* described here. How do so many females organize themselves to excavate such a deep nest? Because old, vacated cells were not found above 170 cm, this nest is not an old one that became deeper with the passing of each generation. What is the basis of the collaboration among nest inhabitants to dig such a deep nest?

Another problem that remains is our ignorance of the basis for the extensive polymorphism associated with the male head capsule. The polymorphism is perhaps most apparent with respect to variation in size (figs. 91, 92), but it also involves head shape. In frontal view small-headed individuals have an oval head shape (fig. 91) with the lateral ocelli (arrow) close to the rear head margin. In large-headed individuals the head is massively quadrate (fig. 92) with the head margin rising abruptly above each compound eye and the lateral ocelli (arrow) are far below the rear margin. Furthermore, the lower frontoclypeal area of the large-headed male is very broad, enhancing the overall quadrate appearance of the head. There is a tendency for small-headed individuals to have the smallest bodies and largest-headed individual to have the largest bodies. Males with intermediate head sizes and shapes are abundant, probably more so than either of the two extremes pictured here.

Why is there such great variability in this feature? Almost certainly it is associated with some other feature such as mating strategy, communal nesting, or another biological attribute yet to be learned.

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